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Comparative water relations in Collembola : transpiration, desiccation tolerance and effects of body size

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Summary :

Transpiration, water content and tolerable water loss were measured in six surface dwelling springtail species. The speed of evaporative water loss was directly proportional to freshweight. Weight specific transpiration of a species was found in good agreement with expectations based on the moisture regime of its optimal habitat. Tolerable water loss was negatively correlated with transpiration rate. Water content appeared to be identical for all species.

Key words : Collembola, transpiration, desiccation tolerance, body size, habitat.

I. Introduction

Distribution and abundance of many species of soil arthropods can be related to the moisture characteristics of their environment (EDNEY, 1977; REMMERT, 1981). The influence of this factor seems to be particularly strong in surface-dwelling springtails (Collembola-Entomobryidae and large Isotomidae) (JOOSSE, 1981). An important feature of these animals is the absence of a tracheal system. Large parts of their integuments are involved in gas exchange which makes them very sensitive to desiccation. Surprisingly, representatives of this group can also be found in rather dry conditions. By consequence the study of differential adaptations to moisture and drought is an important topic in ecophysiology of Collembola.

Recently VERHOEF & WITTEVEEN (1980) reported a relation between transpiration rates of a number of springtail species and water conditions of their optimal habitat. The present communication is an attempt to specify these data by analysing more closely related species and by measuring two additional quantities that seem important in the water economy of springtails : water content and tolerable water loss.

II. Materials and methods

1. Species and habitats

The species used in this study are large Entomobryidae, and *Isotoma viridis* Bourlet. The latter species belongs to a different family but is very similar to the Entomobryidae in its ecology. A species list is provided in Table I, with a short description of optimal habitats with special references to the moisture regime. These descriptions are based on a review by ELLIS (1974) and a faunal survey of more than 50 woodland areas in the Netherlands, to be published by the senior author. The classification of moisture regimes is based on ground water levels and rainfall data.

2. Water content

Water content is expressed as a percentage of fresh weight. The dry weights needed for its computation are determined after one week desiccation at 70° C in Silicagel.

TABLE I

List of species with a short description of their optimal habitat.

Species	Habitat	Moisture regime
Tomocerus minor (Lubbock)	Woodland on clay-like soils	homogeneous, wet
Tomocerus flavescens (Tullberg)	Deciduous woodland on sandy soils with a well-developed litter layer	heterogeneous
Isotoma viridis (Bourlet)	Moist pastures and woodland clearings	homogeneous, wet
Orchesella villosa Geoffroy	Woodland on clay like soils, sparse litter layer	homogeneous, wet
Orchesella cincta (Linné)	Mixed and coniferous woodland on sandy soils	heterogeneous, relatively dry
Orchesella flavescens (Bourlet)	Deciduous woodland on sandy soils *cf. T. flavescens*	heterogeneous

3. Tolerable water loss

Some definition of « tolerable » is needed here. VOLLMER & McMAHON (1974) proposed the use of C.A.P., the critical activity point, defined as the amount of water lost by the test animal when it stops being active, expressed as a percentage of freshweight. C.A.P. can be measured in combination with transpiration measurements (see below). Although it is not sure whether an animal that reaches its C.A.P. is actually dead, it can be considered as such from an ecological point of view, since inactive animals will not be able to leave an unfavorable environment.

4. Transpiration rate

This parameter is defined as the speed evaporative water loss in standardized conditions, corrected for the size of the animal. The speed of water loss is measured as weight loss at 18° C and 0 % R.H. in a closed glass chamber with a layer of Silicagel, attached to a Cahn R.G. electrobalance, connected to a recorder (see VERHOEF & WITTEVEEN, 1980 for more detail). The resulting weight loss registrations are almost straight lines when the animal is alive, indicating that water is lost at a constant speed, and show numerous small spikes when the test animal is active, permitting the determination of C.A.P.

Since the feeding state affects the speed of water loss (VERHOEF, 1981) only feeding adult animals will be used.

5. Correction for body size

The approach adopted here is based on regression analysis. For each species speed of weight loss is regressed on fresh weight. To yield regressions suitable for statistical analysis both variables had to be log transformed. The choice of this transformation was not made for statistical reasons only : log transformation of both variables will yield an allometric regression equation (power function) relating the speed of weight loss to fresh weight. Since transpiration is generally thought to be proportional to the surface area of an animal, the regression equations can be compared with empirically determined (VANNIER, 1977) or theoretical (Meeh's 2/3 Powerlaw; MEEH, 1878) surface-weight relations. The value of the latter relations as a correction for size in interspecific comparisons of transpiration, and current ecological wisdom based on theoretical surface-weight relations (REMMERT, 1981) can be tested.

6. Statistical procedures

Methods for comparisons of regression lines are described by EDWARDS (1979). The analysis of metabolic rates by PETERSEN (1981) provides an example how these methods can be fruitfully applied to problems involving size and shape.

Water content and C.A.P. are analyzed with standard ANOVA methods (see SOKAL & ROHLF, 1969).

III. Results and discussion

1. Water content

In this study no differences in water content were found between species. The mean value, 76 % (95 % confidence interval : 77.24 – 74.64), is in agreement with values for arthropods in general (EDNEY, 1977).

2. Transpiration and body size

The allometric equation relating the speed of weight loss (V) to fresh-weight (W_o) is : $V = a \, . \, W_o^b$, or after logarithmic transformation : $\log V = \log a + b \log W_o$.

Log a and b are parameters to be estimated with linear regression methods. The values of the regression coefficient b obtained for each species were compared and did not differ significantly. The pooled regression coefficient was 1.006 (95 % confidence interval : 0.8 - 1.2). This indicates that the speed of evaporative water loss in springtails is directly proportional to fresh-weight and not to the 2/3 power of fresh-weight predicted by Meeh's formula, or empirically determined surface-weight relations (VANNIER, 1977). Other unexpected « scalings » of transpiration were observed by EDNEY (1971), where speed of water loss approximately proportional to $W_o^{1/3}$ in

desert tenebrionid beetles, and again proportional to fresh-weight in a thysanuran. Clearly the relation between transpiration and body size is not a simple surface-weight relation.

3. Transpiration rate and C.A.P.

Since V appears to be proportional to W_o the use of weight specific transpiration (V/W_o) in interspecific comparisons seems justified. Mean weight specific transpiration (back transformed mean of log (V/W_o)) and mean C.A.P. for each species is displayed in Table II. Values that do not differ significantly at the 5 % level (evaluated with the S.N.K. test procedure; SOKAL & ROHLF, 1969) are underlined. When Table II is compared with the habitat descriptions in Table I the relation between transpiration and habitat moisture conditions appears to be valid as a general trend, but the high transpiration rate of *T. flavescens* is rather unexpected. It should be noted however that woodlands with a well-developed litter- and humus layer are very heterogenous and might provide a sufficient number of moist patches to sustain viable populations of this species.

TABLE II

Mean C.A.P. and weight specific transpiration. Underlined values are not different at p = 0.05.

Transpiration Rate	O. flavescens	O. cincta	O. villosa	I. viridis	T. flavescens	T. minor
Rate $\mu g/mg\ min^{-1}$	0.99	1.0	2.93	6.94	8.48	8.48
Mean C.A.P.	33.84 %	31.55 %	29.98 %	23.83 %	21.76 %	16.20 %

The C.A.P. values in Table II appear to correlated with weight specific transpiration, indicating that fast transpiring species are also more sensitive to dehydration. The C.A.P. of *Tomocerus minor*, however is very low. When this species is dehydrated more gently (VERHOEF, personal communication) much higher values (up to 30 %) can be reached. This suggests that the differences in C.A.P. might be caused by differences in dehydration rate, making the interpretation of C.A.P. as an independent adaptation questionable. As a conclusion we may state that species living in a relatively dry environment tend to restrict water-loss and do not increase their water reserves.

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